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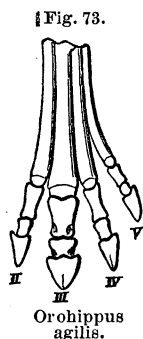
FOSSIL HORSES IN AMERICA.

BY PROFESSOR O. C. MARSH.

IT is a well known fact that the Spanish discoverers of America found no horses on this continent, and that the modern horse (*Equus caballus* Linn.) was subsequently introduced from the old world. It is, however, not so generally known that these animals had formerly been abundant here, and that long before, in Tertiary time, near relatives of the horse, and probably his ancestors, existed in the far west in countless numbers, and in a marvellous variety of forms. The remains of equine mammals, now known from the Tertiary and Quaternary deposits of this country, already represent more than double the number of genera and species hitherto found in the strata of the eastern hemisphere, and hence afford most important aid in tracing out the genealogy of the horses still existing.

The animals of this group which lived in this country during the three divisions of the Tertiary period were especially numerous in the Rocky Mountain regions, and their remains are well preserved in the old lake basins which then covered so much of that country. The most ancient of these lakes—which extended over a considerable part of the present territories of Wyoming and Utah—remained so long in Eocene times that the mud and sand, slowly deposited in it, accumulated to more than a mile in vertical thickness. In these deposits, vast numbers of tropical animals were entombed, and here the oldest equine remains occur, four species of which have been described. These belong to the genus *Orohippus* Marsh, and are all of diminutive size, hardly larger than a fox. The skeleton of these animals resembled that of the horse in many respects, much more indeed than any other existing species, but instead of the single toe on each foot, so characteristic of all modern equines, the various species of *Orohippus* had four toes before and three behind, all of which reached the ground. The skull, too, was proportionately shorter, and the orbit was not enclosed behind by a bridge of bone. There were forty-four teeth in all, and the premolars were smaller than the molars. The crowns of these teeth were very short. The canine teeth were

developed in both sexes, and the incisors did not have the "mark" which indicates the age of the modern horse. The radius and ulna were separate, and the latter was entire throughout its whole length. The tibia and fibula were distinct. In the fore foot, all the digits except the pollex, or first, were well developed, as shown in the accompanying figure (73) of the left fore foot of *Orohippus agilis* Marsh. The third digit is the largest, and its close resemblance to that of the horse is clearly marked. The terminal phalanx, or coffin bone, has a shallow median groove in front, as in many species of this group in the later Tertiary. The fourth digit exceeds the second in size, and the fifth is much the shortest of all. Its metacarpal bone is considerably curved outward. In the hind foot of this genus, there are but three digits. The fourth metatarsal is much larger than the second.



The only species of *Orohippus* at present known are from the Eocene of Wyoming and Utah, and are as follows:—*Orohippus gracilis* Marsh, *O. pumilus* Marsh, *O. agilis* Marsh, and *O. major* Marsh.*

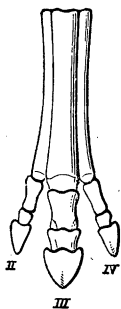
In the middle Tertiary, or Miocene, there were two other lakes on either side of the great Eocene basin. The largest of these was east of the Rocky Mountains, extending over portions of what are now Dakota, Nebraska and Colorado. The clays deposited in this lake form the "*Mauvaises terres*," or "Bad lands," of that region, and are well known for their fossil treasures. The other Miocene lake was west of the Blue mountains, where eastern Oregon now is, but its extent is unknown, as this whole region has since been covered with a vast sheet of basalt, a thousand or more feet in thickness, and the original lake sediments are only to be seen where this lava has been washed away. In both of these ancient lake basins, many remains of animals allied to the horse are found, showing that during the Miocene this group of mammals were well represented.

In the western, or Oregon basin, the genus *Miohippus* Marsh first makes its appearance. It resembles *Orohippus* of the Eocene in its general characters, especially in the shape of the skull, number and form of teeth, and separate ulna; but it had

* American Journal of Science, Vol. vii, p. 247, March, 1874.

only three toes in the fore foot, as well as behind, and the fibula was coössified with the tibia at its lower end. In this genus, all the

Fig. 74.



Miohippus
annectens.

toes reached the ground, as shown in the accompanying figure of the left fore foot of *Miohippus annectens* Marsh, the type species (Fig. 74). In the same deposits, the genus *Anchitherium* Meyer occurs, represented by a single species, *A. anceps* Marsh. This genus is closely allied to *Miohippus*, but differs in having a deep depression in the skull in front of the orbit. The radius and ulna are united, and the outer toes are reduced in size. In the eastern basin, *Anchitherium Bairdi* Leidy is abundant, and with it is found a smaller species, *A. celer* Marsh. The animals of these two genera are all larger than the species of *Orohippus* from the Eocene, some of them exceeding a sheep in size.

The Miocene species known with certainty are as follows:—*Miohippus annectens* Marsh, *Miohippus Condoni* (*Anchitherium Condoni* Leidy) and *Anchitherium anceps* Marsh, from Oregon; and *A. Bairdi*, Leidy, and *A. celer* Marsh, from the eastern basin.

During the Pliocene, or later Tertiary, a great development of the horse family took place, and vast numbers of these animals left their remains in the lake deposits of that epoch. The largest of these lakes had the Rocky Mountains for its western border, and extended from Dakota to Texas, its northern part covering the bed of the older Miocene basin. Another Pliocene lake, of unknown limits, extended over the older Tertiary strata of eastern Oregon, and evidence of still others may be seen in Idaho, Nevada and California. In all of these basins, equine remains of various kinds have been found, but the most important localities are the region of the Niobrara river east of the mountains, and the valley of the John Day river in Oregon.

The equine genera of the Pliocene which appear to be most nearly related to their predecessors from older strata are, *Anchippus* Leidy, *Hipparion* Christol, and *Protohippus* Leidy, all three-toed forms, but with the outer digits reduced to much the same proportions as the posterior hooflets of the modern deer and ox. The genus *Pliohippus* Marsh, from the same deposits, had feet like those of the recent horse. Other genera, less known, which have been proposed, are *Parahippus*, *Merychippus*, and *Hypohippus*

of Leidy, to whose researches we are so largely indebted for our present knowledge of this group. Of these Pliocene genera, more than twenty species have been described from American strata, all apparently larger than their Miocene relatives, but all smaller than the present horse, and many of them approaching the ass in size. Among the more characteristic of these species may be mentioned, *Anchippus Texanus* Leidy, from Texas; *A. brevidens* Marsh, from Oregon; *Hipparion occidentale* Leidy, and *H. speciosum* Leidy, from Nebraska; *Protohippus perditus* Leidy, from the Niobrara; *P. parvulus* Marsh, from Nebraska, the smallest Pliocene species; *Parahippus cognatus* Leidy, and *Pliohippus pernix* Marsh, from the Niobrara.

In the upper Pliocene, or more probably in the transition beds above, there first appears a true *Equus*, and in the Quaternary deposits, remains of this genus are not uncommon. Five or six species are known from the United States, and several others from Central and South America. The latest extinct species appears to have been *Equus fraternus* Leidy, which cannot be distinguished anatomically from the existing horse. These later extinct horses are all larger than the Pliocene Equines, and some of them even exceeded in size the living species.

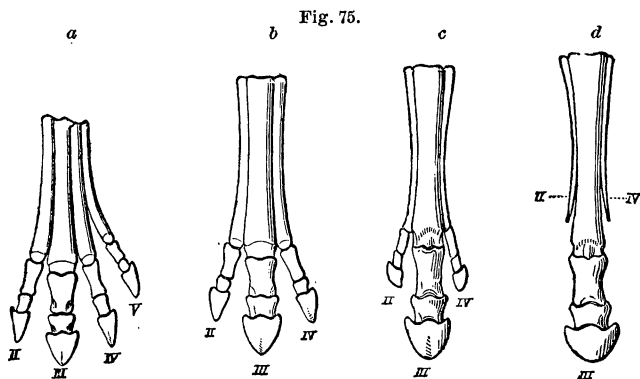
The large number of equine mammals now known from the Tertiary deposits of this country, and their regular distribution through the subdivisions of this formation, afford a good opportunity to ascertain the probable lineal descent of the modern horse. The American representative of the latter is the extinct *Equus fraternus* Leidy, a species almost, if not entirely, identical with the old world *Equus caballus* Linn., to which our recent horse belongs. Huxley has traced successfully the later genealogy of the horse through European extinct forms,* but the line in America was probably a more direct one, and the record is more complete. Taking, then, as the extremes of a series, *Orohippus agilis* Marsh, from the Eocene, and *Equus fraternus* Leidy, from the Quaternary, intermediate forms may be intercalated with considerable certainty from the thirty or more well marked species that lived in the intervening periods. The natural line of descent would seem to be through the following genera:—*Orohippus*, of the Eocene; *Miohippus* and *Anchitherium*, of the Miocene; *Anchippus*,

* Anniversary Address, Geological Society of London, 1870.

Hipparion, *Protohippus* and *Pliohippus*, of the Pliocene; and *Equus*, Quaternary and recent.

The most marked changes undergone by the successive equine genera are as follows: 1st, increase in size; 2d, increase in speed, through concentration of limb bones; 3d, elongation of head and neck, and modifications of skull. The increase in size is remarkable. The Eocene *Orohippus* was about the size of a fox. *Miohippus* and *Anchitherium*, from the Miocene, were about as large as a sheep. *Hipparion* and *Pliohippus*, of the Pliocene, equalled the ass in height: while the size of the Quaternary *Equus* was fully up to that of the modern horse.

The increase of speed was equally marked, and was a direct result of the gradual modification of the limbs. The latter were



a, *Orohippus* (Eocene); b, *Miohippus* (Miocene); c, *Hipparion* (Pliocene); d, *Equus* (Quaternary).

slowly concentrated, by the reduction of their lateral elements and enlargement of the axial one, until the force exerted by each limb came to act directly through its axis, in the line of motion. This concentration is well seen, *e. g.*, in the fore limb. There was, 1st, a change in the scapula and humerus, especially in the latter, which facilitated motion in one line only; 2d, an expansion of the radius, and reduction of the ulna, until the former alone remained entire, and effective; 3d, a shortening of all the carpal bones, and enlargement of the median ones, ensuring a firmer wrist; 4th, an increase in size of the third digit, at the expense of those on each side, until the former alone supported the limb. The latter change is clearly shown in the above diagram (Fig. 75), which represents the fore feet of four typical genera in

the equine series, taken in succession from each of the geological periods in which this group of mammals is known to have lived.

The ancient *Orohippus* had all four digits of the fore feet well developed. In *Miohippus*, of the next period, the fifth toe has disappeared, or is only represented by a rudiment, and the limb is supported by the second, third and fourth, the middle one being the largest. *Hipparion*, of the later Tertiary, still has three digits, but the third is much stouter, and the outer ones have ceased to be of use, as they do not touch the ground. In *Equus*, the last of the series, the lateral hoofs are gone, and the digits themselves are represented only by the rudimentary splint bones.* The middle, or third digit, supports the limb, and its size has increased accordingly. The corresponding changes in the posterior limb of these genera are very similar, but not so striking, as the oldest type (*Orohippus*) had but three toes behind. An earlier ancestor of the group, perhaps in the lowest Eocene, probably had four toes on this foot, and five in front. Such a predecessor is as clearly indicated by the feet of *Orohippus*, as the latter is by its Miocene relative. A still older ancestor, possibly in the Cretaceous, doubtless had five toes in each foot, the typical number in mammals. This reduction in the number of toes may, perhaps, have been due to elevation of the region inhabited, which gradually led the animals to live on higher ground, instead of the soft lowlands where a polydactyl foot would be an advantage.

The gradual elongation of the head and neck, which took place in the successive genera of this group during the Tertiary period, was a less fundamental change than that which resulted in the reduction of the limbs. The process may be said to have already begun in *Orohippus*, if we compare that form with other most nearly allied mammals. The diastema, or "place for the bit," was well developed in both jaws even then, but increased materially in succeeding genera. The number of the teeth remained the same until the Pliocene, when the front lower premolar was lost, and subsequently the corresponding upper tooth ceased to be functionally developed. The next upper premolar, which in *Orohippus* was the smallest of the six posterior teeth, rapidly increased in size, and soon became, as in the horse, the largest of the series. The grinding teeth at first had very short crowns, without cement,

* The modern horse occasionally has one of the ancestral hooflets developed, usually on the fore foot.

and were inserted by distinct roots. In Pliocene species, the molars became longer, and were more or less coated with cement. The modern horse has extremely long grinders, without true roots, and covered with a thick external layer of cement. The canine teeth were very large in *Orohippus*, and in this genus, as well as those from the Middle Tertiary, appear to have been well developed in both sexes. In later forms, these teeth declined in size, especially as the changes in the limbs afforded other facilities for defence, or escape from danger. The incisors in the early forms were small, and without the characteristic "mark" of the modern horse. In the genera from the American Eocene and Miocene, the orbit was not enclosed behind by an entire bridge of bone, and this first makes its appearance in this country in Pliocene forms. The depression in front of the orbit, so characteristic of *Anchitherium* and some of the Pliocene genera, is, strange to say, not seen in *Orohippus*, or the later *Miohippus*, and is wanting, likewise, in existing horses. It is an interesting fact that the peculiarly equine features acquired by *Orohippus* are retained persistently throughout the entire series of succeeding forms. Such, *e. g.*, is the form of the anterior part of the lower jaw, and also the characteristic astragalus, with its narrow, oblique, superior ridges, and its small articular facet for the cuboid.

Such is, in brief, a general outline of the more marked changes that seem to have produced in America the highly specialized modern *Equus* from his diminutive, four-toed predecessor, the Eocene *Orohippus*. The line of descent appears to have been direct, and the remains now known supply every important intermediate form. It is, of course, impossible to say with certainty through which of the three-toed genera of the Pliocene that lived together, the succession came. It is not impossible that the later species, which appear generically identical, are the descendants of more distinct Pliocene types, as the persistent tendency in all the earlier forms was in the same direction. Considering the remarkable development of the group through the entire Tertiary period, and its existence even later, it seems very strange that none of the species should have survived, and that we are indebted for our present horse to the old world.